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Use of eelgrass habitats by fish in eastern Canada

Utilisation des habitats de zostère par les poissons dans l'Est du Canada

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ABSTRACT

The purpose of this document is to review the literature on the ecological function of eelgrass (*Zostera marina L.*) to fish communities in eastern Canada for the purpose of designating eelgrass as an Ecologically Significant Species (ESS). Relatively few studies have investigated the function of eelgrass habitats in eastern Canada compared to the USA or Australia. Therefore, this review also draws from other eelgrass or seagrass studies around the world to demonstrate the use of eelgrass habitats by fish. Eelgrass is a common marine angiosperm that is found in sheltered bays and coastal waters in eastern Canada. Eelgrass meadows provide structural complexity to the nearshore underwater landscape and like seagrass habitats, elsewhere in the world are known to support high densities and diversity of fishes and other aquatic organisms in comparison to unvegetated sandy or muddy bottoms. These habitats are often nursery and rearing areas for young fish. Abundances of juvenile life stages in these habitats are often high, as are those of other small bodied fish. Recruitment to such areas as well as enhanced growth and survival of juveniles over time has led to wide acceptance among ecologists that seagrass habitats are important nursery grounds for many fishes. Several mechanisms seem to explain the high densities of fishes in eelgrass and other seagrass habitats. Among these, refuge from predation, enhanced food resources and habitat structural complexity are generally considered most important to the function of seagrass habitats for fishes particularly juveniles.

RÉSUMÉ

L'objectif de ce document est de passer en revue la littérature sur les fonctions écologiques de la zostère (*Zostera marina L.*) pour les communautés de poissons de l'Est du Canada en vue de désigner la zostère en tant qu'espèce d'importance écologique (EIE). Relativement peu d'études ont été réalisées au sujet des fonctions des habitats de zostère dans l'Est du Canada en comparaison avec les États-Unis ou l'Australie. Ainsi, cet examen se base également sur d'autres études concernant les zostères ou les herbiers marins de partout dans le monde afin de démontrer l'utilisation des habitats de zostère par les poissons. La zostère est une angiosperme marine commune que l'on retrouve dans les baies isolées et les eaux côtières de l'Est du Canada. Les lits de zostère contribuent à la complexité structurelle du paysage sous-marin côtier. Comme les habitats d'herbiers ailleurs dans le monde, il est prouvé qu'ils abritent de fortes densités et une grande diversité de poissons et d'autres organismes aquatiques comparativement aux autres fonds sableux ou vaseux dépourvus de végétation. Ces habitats sont souvent des lieux d'alevinage et de croissance pour les jeunes poissons. On y retrouve souvent une grande abondance de juvéniles et de divers poissons de petite taille. Comme les herbiers présentent un fort recrutement ainsi qu'un taux élevé de croissance et de survie des juvéniles, la grande majorité des écologistes s'entendent pour dire que ces habitats sont d'importantes nurseries pour de nombreux poissons. Plusieurs mécanismes semblent expliquer les hautes densités de poissons dans les habitats de zostère et d'autres herbiers. Parmi les fonctions de ces habitats considérées les plus importantes pour les poissons, et en particulier les juvéniles, on note qu'ils servent de refuge contre les prédateurs, qu'ils contiennent des ressources alimentaires supérieures et qu'ils comportent une structure complexe.

INTRODUCTION

Eelgrass (*Zostera marina* L.) is a common marine angiosperm that grows in shallow coastal waters occurring in subtidal and intertidal regions in eastern Canada (den Hartog 1970; Chambers et al. 1999). Eelgrass meadows provide vertical structural complexity to the nearshore marine landscape and like other seagrass habitats, are known to support high densities and diversity of fishes and other aquatic organisms, compared to unvegetated sandy or muddy bottoms (Orth et al. 1984; Thayer et al. 1984; Heck et al. 1989; Bell and Pollard 1989; Mattila et al. 1999). Marine organisms are not distributed homogeneously. They are often associated with habitats which functionally increase their survival and relevant vital rates. Vegetative cover offers benefits not found associated with barren, but otherwise similar substrates.

Higher faunal abundance, including the recruitment of juvenile individuals into seagrass habitats, favours the growth and survival of fish over time. These common observations, have resulted in numerous investigators identifying seagrass habitats as important nursery grounds for various fishes (Heck and Thoman 1984; Pollard 1984; Thayer et al. 1984; Bell and Pollard 1989; Heck et al. 1989; West and King 1996; Mattila et al. 1999; Heck et al. 2003).

Several mechanisms appear to explain the high abundance of fish in seagrass habitats in general. Refuge from predation, enhanced food resources and habitat structural complexity are generally considered most important to the function of seagrass habitats for fishes (Kikuchi 1980; Stoner 1980; Heck and Orth 1980; Heck and Thoman 1981; Lubbers et al. 1990).

We reviewed the literature on the ecological function of eelgrass to fish communities in nearshore coastal waters in eastern Canada. Eelgrass meets the criteria as an "ecologically significant species" (ESS) (DFO 2009). Relatively little is known about the habitat use of fishes in eelgrass in estuaries of eastern Canada compared to the numerous studies carried out in eastern USA (review in Thayer et al. 1984; Heck et al. 2003) and Australia (review Pollard 1984). However, in recent years, studies on the ecological function of eelgrass in Canadian waters (review Hanson 2004) have produced similar insights into the importance of this marine plant in structuring fish communities in Atlantic Canada (Tupper and Boutilier 1995; Laurel et al. 2003b; Joseph et al. 2006; Grant and Provencher 2007; Bradbury et al. 2008; Cote et al. 2013; Schmidt et al. 2011; Schein et al. 2012) which have all shown greater densities of fish in eelgrass habitats than nearby bare unvegetated habitats. By far, the largest body of research in this field comes from investigations on juvenile Atlantic cod (*Gadus morhua*) and other gadoid fish species and their use of eelgrass as nursery habitat within the coastal zone of Newfoundland (Gotceitas et al. 1997; Grant and Brown 1998; Linehan et al. 2001; Laurel et al. 2003a, 2003b, 2004; Bradbury et al. 2008; Schneider et al. 2008; Gorman et al. 2009) and Nova Scotia (Tupper and Boutilier 1995). These particular species do not occur abundantly in eelgrass beds in the southern Gulf of St. Lawrence (Hanson 1996), likely due to temperature tolerances in these waters. However, the nursery function of eelgrass is strong for other nearshore fish and invertebrate species (Joseph et al. 2006; Schein et al. 2012; Schmidt 2012).

REFUGE FUNCTION OF EELGRASS

Predation has been shown in numerous published studies to be one of the main driving forces in the structuring aquatic communities worldwide; and explains the distribution of fish (especially juveniles) in nearshore coastal waters. High densities of fishes are commonly observed in seagrass beds compared to bare substrate (e.g., Laurel et al. 2003b). Predation is lower in eelgrass beds than unvegetated substrates due to reduced predator foraging effectiveness

(visual and swimming capabilities) in densely vegetated compared to unvegetated areas (Heck and Thoman 1981; Heck et al. 2003; Gorman et al. 2009). Heck and Thoman (1981) showed that predation by mummichog *Fundulus heteroclitus* on grass shrimp *Palaemonetes pugio* is greatly reduced in high density artificial eelgrass (674 shoots/m^2) but not in either medium (464 shoots/m^2) or low density vegetation (274 shoots/m^2). Tethering experiments with Atlantic and Greenland cod (*Gadus ogac*) juveniles in Newfoundland also demonstrated that eelgrass offers greater protection to juvenile cod than unvegetated habitats (Linehan et al. 2001; Laurel et al. 2003a) but patch size (Gorman et al. 2009) and predator density (Laurel et al. 2003a) are also important. Predation risk increases for age-0 cod in fragmented eelgrass habitats compared to larger continuous eelgrass habitats (i.e. small patches of eelgrass beds experience greater predation risk than large patches). This inverse relationship between predation risk and patch size is like due to increased predator foraging efficiency along fragmented edges (Gorman et al. 2009); larger patches have less edge per unit area. Laurel et al. (2004) found that when juvenile cod were found over unvegetated sand substrate, they formed tight aggregations (schooling), in contrast to eelgrass habitats, where they did not school.

FOOD FUNCTION OF EELGRASS

In addition to its anti-predator function, eelgrass also supports greater prey abundance and species richness, compared with non-vegetated habitats in almost all studies. This abundance of prey is thought to promote the occupation of eelgrass habitat, in turn, resulting in increased abundance and diversity of fish species compared to nearby habitats without eelgrass (Lubbers et al. 1990; Schmidt et al. 2011). Below ground, the roots and rhizomes of eelgrass plants provide increased sediment stability (Orth 1977) and benthic habitat complexity. Together with the abundance of food from decaying eelgrass and other associated organic material, eelgrass habitats have been shown to support a richer epifaunal and infaunal community than nearby sandy habitats (Orth 1973, 1977; Stoner 1980). Boström and Bonsdorff (1997) found that the infauna among eelgrass plants and in bare sand substrates was dominated by many of the same taxa but that some species were only found in eelgrass but not adjacent sand substrates. They found that infaunal density and species richness averaged 4 times and 2 times greater, respectively, in eelgrass beds than in bare substrate.

Above ground, eelgrass blades are host to a variety of epiphytic flora and fauna (Schneider and Mann 1991; Neckles et al. 1993; Boström and Bonsdorff 1997; Schmidt et al. 2011; Schmidt et al. 2012; Schmidt 2012). By reducing water flow, eelgrass beds act as traps for sediments (Fonseca et al. 1982; Ackerman and Okubo 1993) and invertebrate species whose larvae or propagules drift as passive particles. The settlement of macroscopic epiphytic algae on the blades of *Zostera* creates another level of habitat complexity and also serves to further trap particles. The most common macroscopic algae found on eelgrass leaves in Atlantic Canada are the filamentous green algae, *Ulothrix* spp. and *Polysiphonia* spp. (Schmidt et al. 2012), which grow in dense or highly branched clumps providing refuge to small and highly mobile herbivores such as amphipods (Hacker and Steneck 1990; Schneider and Mann 1991).

The quality of marine vegetated areas as foraging grounds has not been widely investigated. Living eelgrass itself is rarely consumed by fishes and decapods; however, the rich fauna associated with eelgrass habitats are potential prey for many fish and invertebrate species (Kikuchi 1980). Orth and Heck (1980) found that fish fed on epifaunal invertebrates found within eelgrass habitats and Adams (1976c) reported that 56% by weight of diet consumed by eelgrass-associated fishes is found in the same habitat. Renkawitz et al. (2011) did not always observe this outcome, but when significant differences in growth rate were observed in their

experimental cage experiments, juvenile fish caged in eelgrass usually grew fastest, compared with barren seabeds and especially with pelagic habitat.

In a more elaborate quantitative study done by Sogard (1992), growth rates of three species of estuarine-dependent fish (winter flounder *Pseudopleuronectes americanus*, tautog *Tautoga onitis* and naked goby *Gobiosoma bosci*) were compared in vegetated versus unvegetated habitats in New Jersey estuaries. Only the naked goby seemed to show an obvious trade-off between foraging and predator avoidance by living in eelgrass, which was a poor habitat for growth but provided refuge from predation. A similar explanation has been offered for distribution of juvenile cod among sites with variable eelgrass landscape complexity in Newfoundland (Thistle et al. 2010). Both winter flounder and tautog showed no obvious trade-off between growth and predation in both unvegetated and vegetated areas; but lived where growth rate was highest. Winter flounders were better able to exploit sandy substrates due to their cryptic coloration and burying abilities, and thereby may have avoided predation in the more open habitats (Sogard 1992). In tidal freshwater marsh creeks, Rozas and Odum (1988) found that bluespotted sunfish (*Enneacanthus gloriosus*) and killifish (*Fundulus* spp.) eat a greater variety of and larger size of prey in vegetated enclosures compared to unvegetated areas. Their study concluded that submerged aquatic vegetation both served as refuge from predation and provides a rich foraging habitat.

HABITAT COMPLEXITY FUNCTION OF EELGRASS

Although predation is recognized as a key force organizing seagrass communities, other factors such as the physical or structural complexity of habitats can contribute to faunal richness and abundance in seagrass habitats. Components of habitat complexity include above ground biomass, shoot density, plant species richness, and spatial heterogeneity of eelgrass beds (Schneider et al. 2008). Above ground plant biomass can be a reasonable indication of habitat complexity as it is associated with available living space; although there may be specific instances where abiotic conditions (high temperature, low oxygen) become unfavorable (Heck and Orth 1980; Orth and Heck 1980). Seasonal abundance of fishes also correlates with plant biomass which increases over spring and summer and decreases in the fall (Szedlmayer and Able 1996). Density of plant shoots can indirectly affect predation rates in seagrass communities and a nonlinear relationship exists between predation and shoot density. High densities of shoots can impair a predator's foraging success, indicating a threshold density of seagrass at which predators are no longer efficient in capturing prey (Heck and Thoman 1981; Gotceitas and Colgan 1989). Habitats with other components, such as drift algae (higher plant biomass and spatial heterogeneity), can support more diverse and abundant fauna than homogeneous meadows of seagrass because of their associated microhabitats (reviewed by Heck and Orth 1980) and since tested and confirmed by Schneider et al. (2008) and Thistle et al. (2010).

Increased habitat heterogeneity can also result from bare patches (caused by wave action, boats, ice scour and plant senescence) within homogeneous patches of seagrass (Schneider et al. 2008; Thistle et al. 2010). These bare patches are potentially important for mobile fauna by providing foraging corridors through eelgrass beds in close proximity to shelter in seagrass habitats. This type of heterogeneity was important for juvenile red drum (*Sciaenops ocellatus*) which was more abundant in patchy areas than in homogeneous stands of a tropical seagrass, *Halodule wrightii* (Holt et al. 1983) and has been speculated to explain the distribution of juvenile Atlantic and Greenland cod in fragmented eelgrass habitats in some Canadian waters (Schneider et al. 2008; Gorman et al. 2009; Thistle et al. 2009). Stoner (1983) found habitat heterogeneity offered by patchy distribution of low plant biomass (9.3 g dry wt/m^2) and

occasional clumps of red algae and sponges supported the highest species richness of fishes in comparison to other more densely monospecific vegetated sites. Szedlmayer and Able (1996) noted higher species richness of fishes in the most structurally heterogeneous environments (dense stands of eelgrass and an associated red sponge *Microciona prolifera*) than in less heterogeneous natural and dredged sandy channels.

NURSERY FUNCTION OF EELGRASS

A nursery habitat for a particular species is defined by its greater contribution per unit area to the production of individuals that recruit to adult populations relative to other habitats where juveniles of that species are found. The ecological processes operating in a nursery habitat that contribute to greater recruitment to adult populations must include any combination of the following four factors: 1) higher densities, 2) faster growth rates, 3) increased juvenile survival, and 4) greater movement to adult habitats (Gillanders et al. 2003; Heck et al. 2003). Our review has highlighted the importance of eelgrass as nursery habitats in eastern Canada for each of these four factors.

Effect of eelgrass on juvenile abundance

Eelgrass adds spatial complexity above and below the substratum creating a 3-dimensional habitat that contributes to the higher density of juvenile fishes than adjacent unvegetated areas in eastern Canada (Joseph et al. 2006; Grant and Provencher 2007; Laurel et al. 2003b; Bradbury et al. 2008; Schmidt unpublished data). Joseph et al. (2006) found juvenile cunner (<3cm) and white hake only in eelgrass beds in Kouchibouguac Estuary, NB. Grant and Provencher (2007) also found a high proportion of juveniles in their study of eelgrass beds in the upper St. Lawrence Estuary in Quebec. Eelgrass beds in the Gulf of St Lawrence also have high numbers of adults and juveniles of forage fishes such as mummichogs, Atlantic silversides (*Menidia menidia*) and fourspine (*Apeltes quadracus*) and threespine sticklebacks (*Gasterosteus aculeatus*) that are important diet components for many large fish species (Schmidt 2012). In addition, mummichogs and threespine sticklebacks are known to spawn in eelgrass beds (Schein et al. 2012) making these beds essential for the reproduction of these particular forage fish species. Bradbury et al. (2008) also found elevated numbers of juvenile cod in eelgrass compared to adjacent sandy sites in Newfoundland. A similar pattern is seen from seine catch data from eelgrass and non-eelgrass sites in Newman Sound, Newfoundland collected over a 14 year period, 1996-2009 (Fig. 1). Large scale habitat manipulations from 1995-2001 in waters off Newfoundland have conclusively shown the nursery function of eelgrass habitats to juvenile cod. Two species of cod, Greenland cod and Atlantic cod, abundance increased at sites enhanced with artificial eelgrass and decreased at sites where eelgrass was removed relative to years before habitat manipulations (Laurel et al. 2003b).

Some species whose planktonic stages are capable of swimming (decapod crustaceans and fish) may even preferentially settle in eelgrass beds, while others actively migrate into the habitat post-settlement. In Newfoundland, both the Atlantic cod and Greenland cod delayed settlement until they encountered preferred eelgrass habitat (Laurel et al. 2003b, 2004). Recently settled Atlantic and Greenland cod (age 0) were able to differentiate between habitats of varying quality and were found almost exclusively in eelgrass (Gotceitas et al. 1997) or artificial eelgrass mimics (Laurel et al. 2003b). However, in Nova Scotia, juvenile cod did not appear to have a preference for a particular structured habitat type at settlement but juveniles were more abundant in eelgrass compared to unstructured sand substrates following settlement to the seabed (Tupper and Boutilier 1995).

Effect of eelgrass on individual growth

Growth is a critically important factor affecting the demography of juvenile and adult fishes and crustaceans. It directly influences adult population size by controlling the number of individuals reaching reproductive maturity but also indirectly through the effects of size-selective mortality on juvenile survival (Sogard 1992; Perkeins-Visser 1996). Rapid growth means less time spent in the smaller, more vulnerable size classes (Perkeins-Visser 1996; Sogard 1997) and larger sizes increases over-winter survival in temperate fishes (Sogard 1997).

A meta-analysis of growth data found that in general growth rates were significantly higher in seagrass than unvegetated habitats (Heck et al. 2003). Overall, the growth rates of the temperate species Atlantic cod, cunner *Tautogolabrus adspersus* , blue crab, *Callinectes sapidus*, and tautog, all showed higher juvenile growth rates in eelgrass compared to all other habitats tested (Tupper and Boutilier 1995, 1997; Heck et al. 2003). Enclosure experiments in Newman Sound, Newfoundland (Renkawitz 2008) have shown that growth of young cod and hake can be higher in eelgrass than either nearby barren substrates or pelagic habitats. However, results of growth and feeding have not been unequivocal. Thistle et al. (2010) reported that juvenile Greenland cod in moderately fragmented eelgrass habitats showed higher prey consumption rates than either sites with low amounts of eelgrass or eelgrass meadows. Despite its higher abundances in eelgrass beds, goby were found to have lower growth rates in the eelgrass than in unvegetated areas suggesting that this species is sacrificing rapid growth by residing in the beds, which is thought to be a trade-off for refuge (Sogard 1992). The growth rate of winter flounder was also lower when maintained in cages in eelgrass than in unvegetated habitats where they are naturally more abundant (Sogard 1992; Heck et al. 2003).

Effect of eelgrass on juvenile survival

Predation can be a major determinant of the abundance and distribution of species, as well as influencing community structure (Paine 1966). Experimental evidence suggests that seagrasses in general affect predator-prey interactions (Heck et al. 2003). The presence of eelgrass shoots has been shown to significantly reduce the effectiveness of visual predators on epifaunal invertebrates and fish relative to unvegetated habitats (Heck et al. 2003).

In Nova Scotia, the predation efficiency of cottids, such as the sea raven *Hemitripterus americanus* and long horn sculpin *Myoxocephalus octodecemspinosus*, on recently settled Atlantic cod and cunner decreased with increasing habitat complexity and was significantly lower in eelgrass than in unvegetated habitats (Tupper and Boutilier 1995, 1997). However, survival rates among the structurally complex habitats tested were lowest in eelgrass suggesting that eelgrass beds do offer some protection but are not necessarily the best refuge among those available for newly settled cod and cunner (Tupper and Boutilier 1995, 1997). In Newfoundland, predation rates on juvenile Atlantic cod were negatively correlated with eelgrass patch size even though predator abundance showed the opposite trend (Laurel et al. 2003a). However, unlike Nova Scotia, no juveniles were observed in areas of coarse bottom with macroalgae because of the presence of larger piscivorous conspecifics. Cod are known to be cannibalistic and the avoidance by age 0 cod of coarse substrate frequented by older juveniles may represent predator avoidance via size-class segregation (Gotceitas et al. 1997). Overall, these results suggest that eelgrass beds offer an important refuge from predation and cannibalism for juvenile cod in Atlantic Canada. In the southern Gulf of St. Lawrence, water temperatures in areas that support eelgrass are too warm during the summer and Atlantic cod do not utilize eelgrass habitat at all (Hanson 1996).

EVIDENCE OF MOVEMENT TO ADULT HABITAT

As noted by Gillanders et al. (2003), a critical missing link in our understanding of the role of nurseries in marine environments is the connectivity between juvenile and adult habitats. Gregory et al. (2006) found that there was good correspondence between age-classes of juvenile Atlantic cod based on the abundance of segregated age 0 and age 1 cod cohorts. The link to the offshore adult cod populations has remained elusive, as it does for many of the species using eelgrass habitats. However, there has been shown to be a statistically strong correlation between age 1 cod abundance in Newman Sound and the age 3 abundance in the Sequential Population Analysis (SPA) in inshore coastal areas of Newfoundland (DFO 2007), noted in several years following the 2007 stock assessment. Although evidence for movement from eelgrass to adult habitat is currently lacking, there is strong support that the other three ecological processes that define nursery habitats are operating in eelgrass habitats for a range of marine species (Cote et al. 2013) and by extension are likely contributing to greater recruitment of these species to adult populations.

CONCLUSION

Ecologically, eelgrass in eastern Canada functions in a similar fashion to better studied seagrass beds located in the eastern USA and in Australia. Eelgrass habitats are known to support high densities and diversity of fishes and other aquatic organisms in comparison to unvegetated sandy or muddy bottoms. Eelgrass, through its emergent structure, provides structural complexity to the underwater coastal landscape (Chambers et al. 1999). For fishes, this complexity in the marine and estuarine environment provides cover from predation, provides an abundance of prey for foraging fish and serves a nursery role in recruitment, growth and survival of juveniles and likely contributes to movement into adult habitat.

Eelgrass has been identified as an ecologically sensitive habitat due to its constrained range of physical, biological and chemical factors favorable for its growth and its susceptibility to harm by human activities (Vandermeulen 2005). Some current threats to eelgrass include eutrophication and invasive species such as green crabs. Eutrophication can cause dramatic declines in eelgrass abundance and its loss has been linked to virtually all areas of intense human settlement (Lotze et al. 2006). The replacement of eelgrass with mats of opportunistic algal species such as green lettuce (*Ulva*) and other filamentous forms alters the species composition (Borg et al. 1997; Lotze et al. 2004) and by extension the functions of these coastal habitats. The introduction of the green crab to the central eastern coast of the United States in the late 1800's and subsequent spread northward into Canadian waters has had significant impacts in coastal estuaries (D.J. Garbary, St. Francis Xavier Univ. personal communication) and raised some alarm in the northern portions of the plant's range (Morris et al. 2010). During foraging, the crabs have been shown to tear and cut at the eelgrass shoots leading to shoot loss (Davis et al. 1998). They also burrow into the sediments, potentially weakening the root and rhizome system that anchor eelgrass into the sediments making the eelgrass more vulnerable to loss due to storms or other disturbances.

Eelgrass is a dominant feature of estuaries and coastal marine environments in eastern Canada providing numerous ecosystem functions and services (Chambers 1999; Vandermeulen 2005; Schmidt et al. 2011; Schmidt et al. 2012). There is no replacement for eelgrass in soft sediment habitats therefore its loss will have profound consequences on the trophic dynamics and services of estuaries disproportionate to its spatial coverage within a geographic area (Schmidt 2012). This fact alone warrants the careful management and protection of this ecologically significant species.

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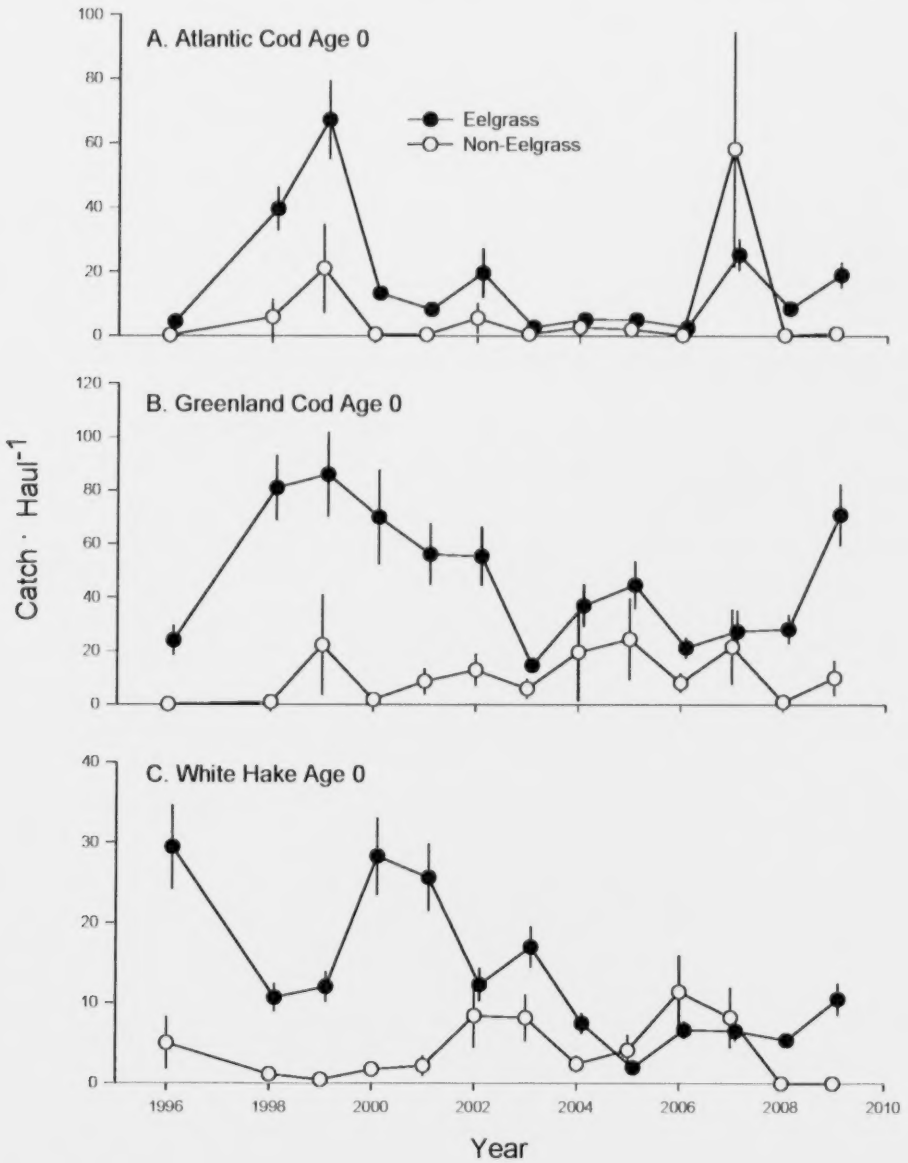

Figure 1. Mean catches of (A) age 0 juvenile Atlantic cod, (B) Greenland cod, and (C) White hake collected by demersal seine net over eelgrass and sand/gravel substrates, in Newman Sound, Newfoundland, 1995-2009. Catch data are mean catch per haul (seine set = 880·m^{-2}; vertical bars are ± s.e.), during an annual total of 75-132 biweekly seine hauls made July-November each year. In 2005-2007, eelgrass was becoming established in a formerly non-eelgrass site, explaining a substantial increase in abundance of juvenile Atlantic cod and white hake in "non-eelgrass" habitat. For methods see Gregory et al. (2006).